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The Phylogeny of the Felidae.

BY W. D. MATTHEW.



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(Continued from 3d page of cover.)

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Article XXVI.—THE PHYLOGENY OF THE FELIDÆ.

By W. D. MATTHEW.

Fossil members of the cat family have been found in all the principal horizons of the Middle and Later Tertiary, and in the Pleistocene. Some of them equal or exceed in size the largest living species; none are smaller than the modern domestic cat. The great majority, including all of the more ancient species, are distinguished by greater or less enlargement of the upper canines into long curved and flattened tusks. These are the Sabre-tooth Tigers, well known to popular science. True cats in which the upper and lower canines are of nearly equal size, are not known as fossils until the Pliocene.

The oldest of the Macharodonts or Sabre-tooth Tigers are found in the Lower Oligocene of Europe and North America. In both countries these oldest forms are comparatively large animals, ranging from leopard to lynx size, and are clearly divided into two series, one with very long but slender canines, protected by a deep flange on the lower jaw, the other with shorter canines and much less flange on the jaw. The best known member of the first series is *Hoplophoneus*, of the second *Dinictis*, both represented in American Museums by several complete skeletons and many skulls from the White River and John Day Oligocene. The European genera *Eusmilus* and *Elurictis* are closely related to the better known American forms.

No Eocene carnivora are known from which either of these Oligocene Sabre-tooths can be derived. Their supposed derivation (Wortman, 1892) from *Palaonictis* (Lower Eocene) through *Elurotherium* (Middle Eocene) has been shown (Matthew, 1909) to be erroneous, *Elurotherium* being founded on the milk dentition of *Patriofelis*, which like *Palaonictis*, is a member of the Oxyænidæ, a family of Creodonts in which the carnassial specialization affects a different pair of teeth ($\frac{m_2^1}{m_1^1}$) from the pair involved in the specialization of all modern carnivora ($\frac{p_1^1}{m_1^1}$). The earlier derivation from *Oxyana* itself (Cope, 1880) is invalid for the same reason. *Proxlurus* has been regarded by some authors as representing an early stage in the structural evolution of the cats, but it is less ancient than *Hoplophoneus* or *Dinictis* and therefore of no genetic significance, and is furthermore probably rather of Mustelid than Felid affinities.

The successors of *Dinictis* and *Hoplophoneus* in the Upper Oligocene are *Nimravus* and *Eusmilus*, closely related to their predecessors, with somewhat more specialized dentition; but in *Nimravus* the upper canines

are shorter than in *Dinictis*.¹ In the Miocene, *Pseudalurus*² and *Macharodus* are the probable successors; both genera are imperfectly known and chiefly from European specimens. In the Pleistocene of North America,³ and in the Pliocene and Pleistocene of Europe, we find true cats of the genus *Felis*, and gigantic and highly specialized sabre-tooths of which *Smilodon* is the best known representative.

While the derivation of the great Pleistocene Sabre-tooths from the Oligocene *Hoplophonus* has been generally accepted, the exact relationship of the less specialized series of primitive sabre-tooths represented by *Dinictis*, has not I think been correctly appreciated. They have been regarded as early stages in the specialization of the sabre-tooth series, while the true cats have been derived from undiscovered Oligocene Felidae with normal canines. The evidence appears, however, to indicate that the *Dinictis* phylum led directly into the modern Felidae, the canines having reverted from the almost unique macharodont specialization to the normal type of carnivorous mammals. The series *Dinictis-Nimravus-Pseudalurus-Felis* are in direct succession, structurally and geologically.

The difference in length of canines between the Dinictid and Hoplophoneid series of sabre-tooths is correlated with a large number of well marked and constant distinctions in the structure of teeth, skull and skeleton. In every one of these characters the Dinictid series agrees with the true cats or is structurally ancestral to them: while the Hoplophoneid series agrees with the great Pleistocene sabre-tooths or is ancestral to them.

I. The dentition in the two series is as follows:

<i>Felis</i>	3.1.3-2.1 3.1.2.1	<i>Smilodon</i>	3.1.2.1 3.1.2-1.1
<i>Pseudalurus</i>	3.1.3.1 3.1.3-2.1	<i>Macharodus</i>	3.1.2.1 3.1.2.1
<i>Nimravus</i>	3.1.4.3.1 3.1.3-2-2.1	<i>Hoplophonus</i>	3.1.2-3.1 3.1.2.1
<i>Dinictis</i>	3.1.4.3.1 3.1.3.2		

Carnassial Specialization and Molar Reduction.

II. The construction of the carnassials affords a ready means of distinguishing the two series. In *Dinictis* and its successors the two principal blades of the upper and lower carnassial are separated by a deep, sharply

¹ *Archalurus* is not generically separable from *Nimravus*, auct. J. C. Merriam, 1906. *Pogonodon* I regard as a distinct subgenus.

² *P. quadridentatus* (type) of the Middle Miocene (Sansan) of Europe. *P. intrepidus* of the Upper, and *P. sp. indesc.* of the Middle Miocene of North America, but exclusive of *P. edwardsi* of the Phosphorites, which I refer to *Elurictis*.

³ *Felis hillanus* of the North American Pliocene (Blanco) is not generically determinable as the dentition is unknown. The same remark applies to all other recorded occurrences of *Felis* in the American Miocene or Pliocene.

cut notch, identical in type with that in all modern felines. In the Hoplophoneid series the notch in the upper carnassial is shallower, and the blades more nearly continuous.

In the upper carnassial of *Dinictis* the external blades are composed of two cusps (paracone and metacone), as in the Canidae and Mustelidae and most primitive carnivora; there is also a distinct internal cusp (protocone). In the successive stages a third antero-external cusp (parastyle) is developed,

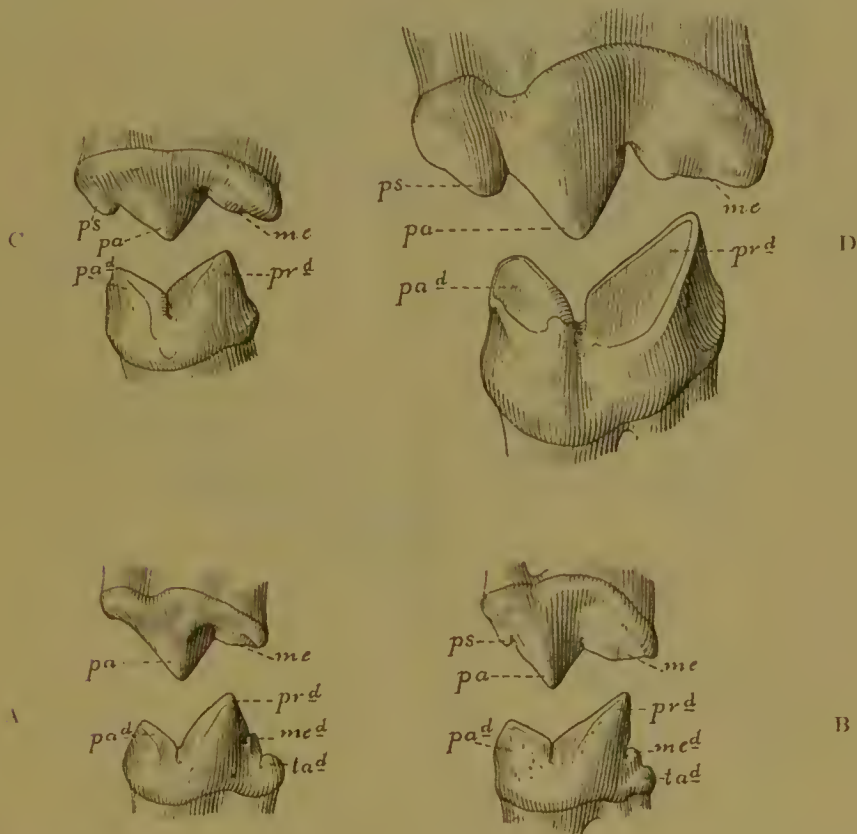


Fig. 1. Carnassials of Felines and Machærodonts. A, *Dinictis*; B, *Hoplophoneus*; C, *Felis*; D, *Smilodon*. All natural size. Upper carnassials: *me*, metacone; *pa*, paracone; *ps*, parastyle. Lower carnassials: *me^d*, metaconid; *pa^d*, paraconid; *pr^d*, protoconid; *ta^d*, talonid or "heel." From the specimens illustrated in Figs. 10, 13, 12, and 15.

rudimentary in *Pseudalurus*, distinct in *Felis*, while the internal cusp becomes less separate, although still retained. In *Hoplophoneus* we find in addition to the two principal external cusps, a small antero-external (parastyle) which develops to large size in *Machærodus*, and in *Smilodon* a fourth external cusp is frequently developed in front of it; but these cusps are always more closely connected with the paracone, forming more of a continuous blade, than in the *Dinictis-Felis* series. The inner cusp is

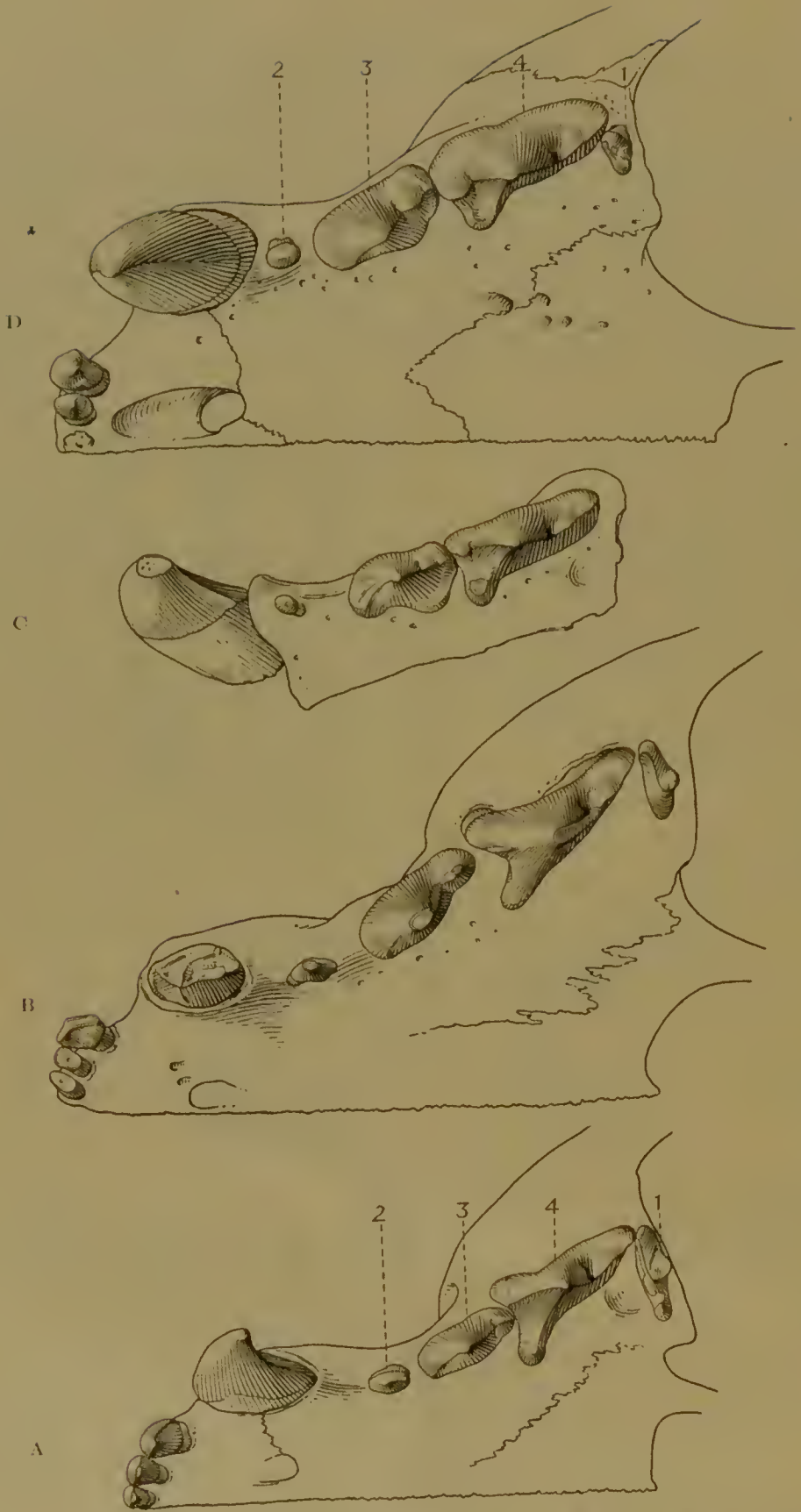


Fig. 2 Feline series, upper jaw. A, *Dinictis*, No. 8777, Middle Oligocene; B, *Nimravus*, No. 6931, Upper Oligocene; C, *Pseudalurus* (after Filhol), Middle Miocene; D, *Felis*, No. 11082, Recent. All natural size.

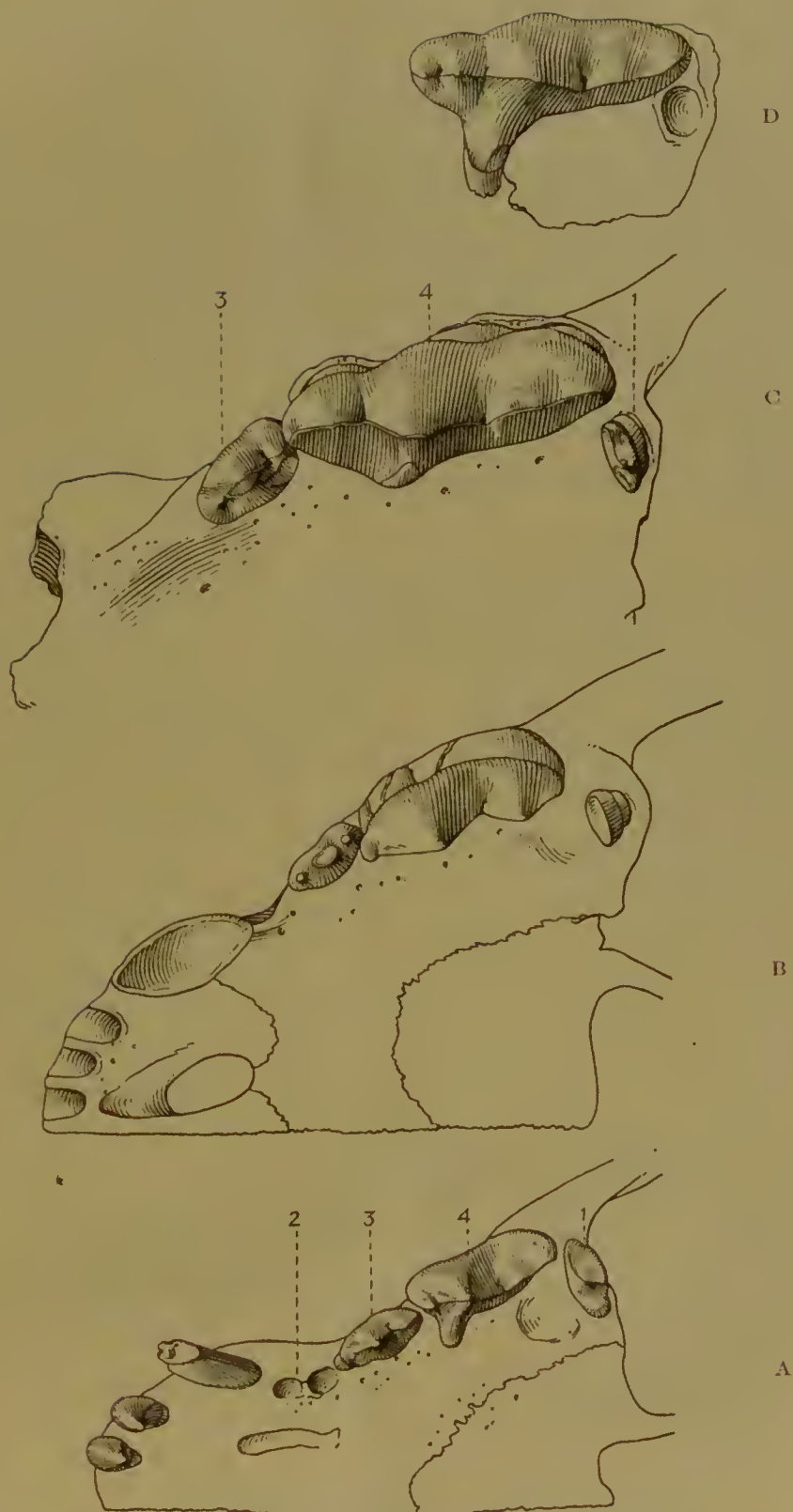


Fig. 3. Macharodont serles, upper jaws. A, *Hoplophontius*, No. 9764, Oligocene; B, *Macharodus* (after Filhol), Miocene; C, *Smilodon*, No. 14349, Pleistocene; D, *Trucifelis*, No. 10395, Pleistocene. All natural size.

always vestigial or absent in the *Hoplophonus-Smilodon* series, although there is usually an inner root to the carnassial.

The lower carnassial of *Dinictis* has a distinct heel and usually a vestigial metaconid. In *Nimrurus* (and *Elurictis*) the metaconid has entirely disappeared but the heel is still distinct. In *Pseudalurnus* the heel is vestigial, and it has entirely disappeared in *Felis*. *Dinictis* has also a vestigial m_2 , minute to absent in its successor *Nimrurus*, absent in the later stages. *Hoplophonus* has a very small vestigial heel and metaconid on the lower carnassial, but no m_2 ; this heel and metaconid have vanished in all the later stages of the machærodont phylum.

The upper molar is reduced in both series *pari passu*, from a fairly well developed transverse cutting tooth to an oval vestigial tooth of very small size.

III. *Premolar Reduction.* The mere enumeration of the premolars fails to show the real difference in the premolar dentition of the two phyla. In the Dinictid-Feline phylum the essential functional premolars are two of subequal size in the lower jaw, and one large premolar in front of the upper carnassial opposes them. In the Machærodont phylum there is but one large premolar in the lower jaw and a small premolar in front of the upper carnassial. The remaining premolars are vestigial and successively disappear.

In the Dinictid phylum, p^1 is vestigial or absent in *Dinictis* and *Nimrurus*, absent in *Pseudalurnus* and *Felis*. P^2 is small in *Dinictis*, vestigial in *Nimrurus* and *Pseudalurnus*, vestigial or absent in *Felis*. P_2 is vestigial in *Dinictis*, vestigial or absent in *Nimrurus* and *Pseudalurnus*, absent in *Felis*.

In the Machærodont phylum, p^2 is vestigial or absent in *Hoplophonus*, usually absent in the later stages. P_3 is small in *Hoplophonus*, vestigial in *Machærodus* (absent in the later species), usually absent in *Smilodon*.

IV. *Proportions of the Skull.* *Dinictis* and its successors have throughout the characteristic feline outlines and proportions in the skull. The frontal region is high, the occiput rather broad and low, the basicranial region wide and flat and nearly in a plane with the palate; the glenoid articulations are nearly in a plane with the basicranial surface. When viewed with the alveolar borders in the horizontal plane the skull is usually highest at the frontal region, sloping downwards towards the occiput and muzzle.¹

In the Hoplophoneid phylum the skull, when oriented in the same way, is highest at the occiput, with a convex downward slope from that point

¹ In the accompanying drawings the skulls are referred to a horizontal plane passing through the premaxillary border and the glenoid articulations for the lower jaw. This is approximately the plane of the alveolar borders and of the hard palate.

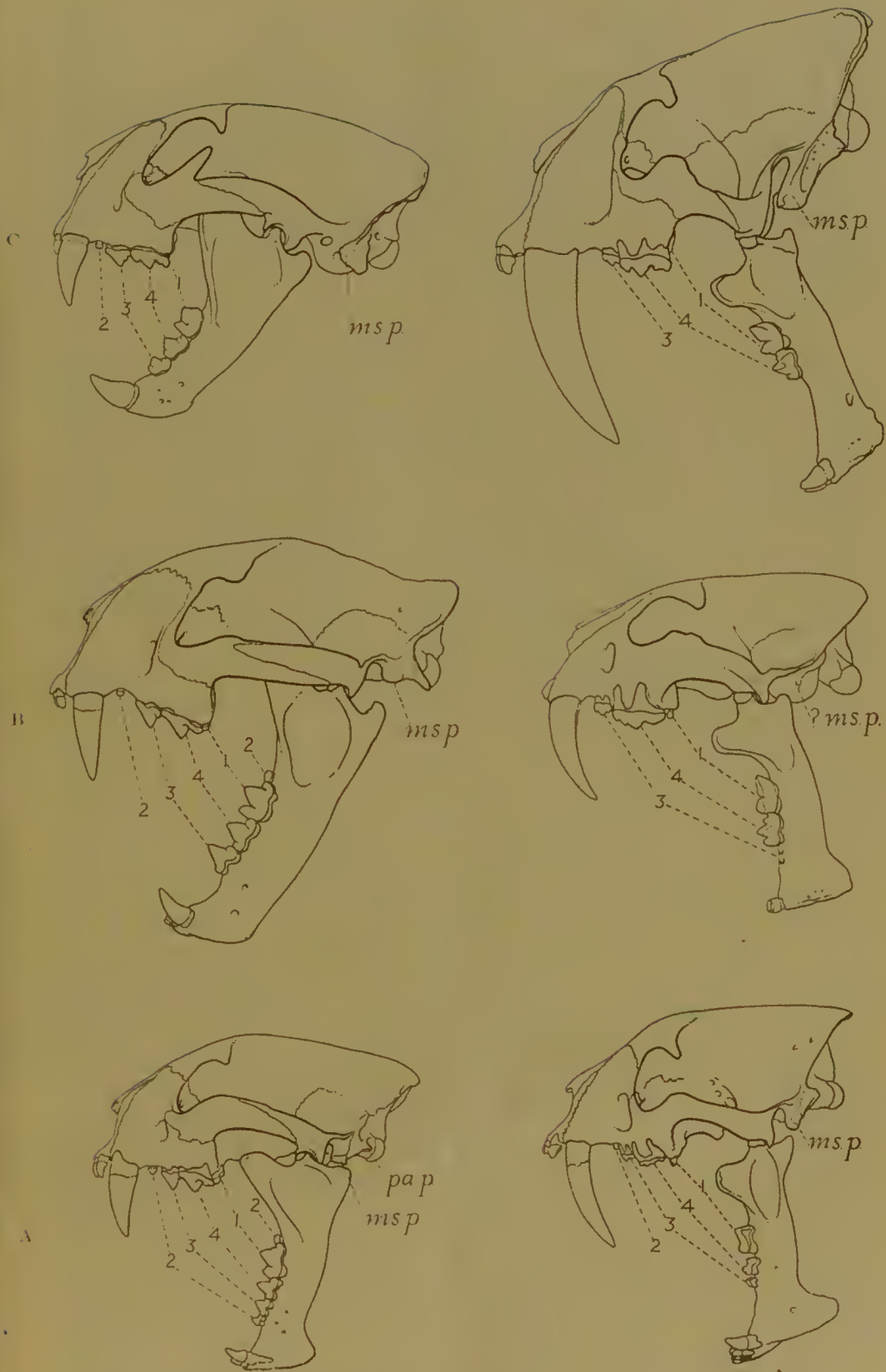


Fig. 4. Skulls of Felines and Machærodonts. A, *Dinictis* and *Hoplophonus*; B, *Nimravus* and *Machærodus*; C, *Felis* and *Smilodon*.

to the nasals. The condyles and basicranial region lie in a considerably higher plane than the palate, and the glenoid articulations are much below the level of the basicranial plane. The occiput is comparatively high and narrow, the condyles very prominent and convex, and their facets continued forward upon the inferior surface of the basicranium. The zygomatic arches are much shorter than in the Dinictid-Feline phylum and are widest at the glenoid articulations. The brain-case is relatively much smaller.

V. *Development of the Mastoid Process.* In *Dinictis* this process is distinct and prominent, but small. In *Nimravus* it is less prominent. In *Pseudalurus* this part of the skull is unknown. In the modern cats the mastoid process is merely a small convex rugosity. On the other hand in the macharodont series it is at first, in *Hoplophonus*, of larger size than in *Dinictis* and more prominent, but similar in form and position. In the successive stages of *Macharodus* and *Smilodon* it progressively increases in size and prominence, encroaching and projecting more and more towards the postglenoid process, and reaching its maximum both of size and of distance in front of the occipital condyles in *Smilodon*.

The development of this process is directly dependent upon the greater or less size of the *cleido-mastoid* muscle, which originates at the tip of the mastoid process and is attached to the anterior border of the clavicle. Closely associated with this muscle in function is the *sterno-mastoid*, originating upon the postero-lateral exposure of the mastoid bone and attaching to the anterior end of the sternum. The function of these muscles is to pull the head forward and downward upon the neck. In the cats they are quite small, and their leverage, measured by the distance of the mastoid process in front of the occipital condyles, is short. In *Smilodon* the scars of their origin, the cleido-mastoid upon the tip, the sterno-mastoid upon the side of the mastoid process (the origin of the muscle having apparently moved downward and forward along the mastoid exposure) shows them to have been (1) enormously powerful muscles, with (2) much greater leverage for direct downward movement of the skull than in the cat. This enabled the Sabre-tooth to strike a (1) tremendously powerful, (2) quick downward blow with the great canine tusks.

Coördinated with the development of the sterno-cleido-mastoid muscles is a corresponding development of the scalene muscles of the neck, passing from the transverse processes of the cervicals to the lower ends of the anterior ribs. In the Macharodont series the origins of these muscles are progressively enlarged, as indicated by the transverse processes, which are progressively converted into long stout spines, directed backward, downward and outward; in the feline series they are progressively reduced,

the transverse processes reverting to the normal type of a thin flat plate of bone. Usually these scalene muscles chiefly serve to draw the ribs forward and upward and so expand the chest; but in combination with other body-muscles they would equally serve to pull the neck downwards, and this I take to have been their chief function in *Machærodonts*.

VI. *Basiscranial Characters*. Both *Dinictis* and *Hoplophoneus* have a

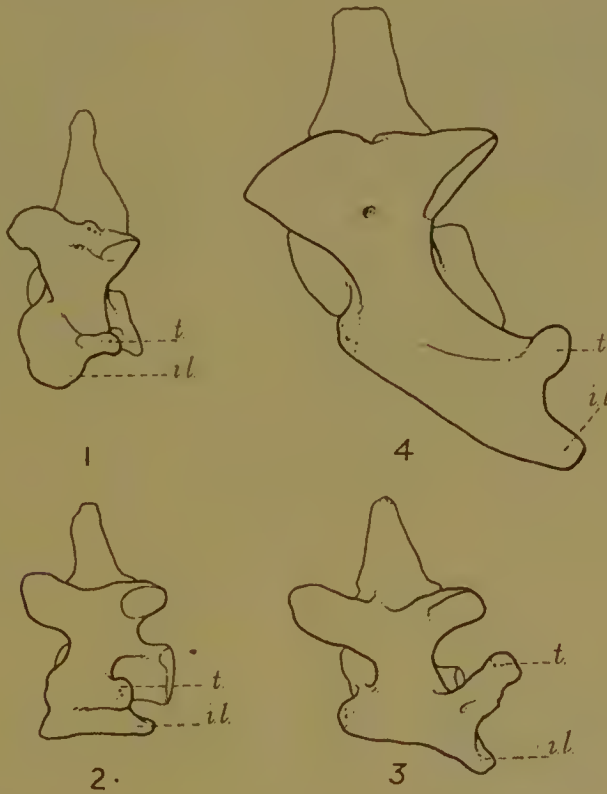


Fig. 5. Fifth cervical vertebra in Felines and *Machærodonts*. 1, *Dinictis*; 2, *Felis*; 3, *Hoplophoneus*; 4, *Smilodon*. All one half natural size. T, transverse process; i-l., inferior lamina.

number of important features in the basiscranial region, in which they differ from either *Smilodon* or the modern felines, and approach the more generalized or primitive carnivora.

1. The condylar foramen is always, and the carotid canal generally, wholly distinct from the posterior lacrate (jugular) foramen.
2. An alisphenoid canal is present.
3. A postglenoid foramen is present.
4. The paroccipital process is directed backwards and free from the tympanic bulla.
5. The tympanic bulla is never completely ossified.

All of these are features characteristic of the Eocene Creodonta.¹ Some of them are retained in one or another group of the modern carnivora. All of them are lost by the Pliocene, Pleistocene or modern cats and Machærodonts.

Upon these primitive basicranial characters and upon additional primitive characters observable in the skeleton Cope based his family Nimravidae. His characterization of them as False Sabre Teeth shows however that he did not regard them as constituting simply a primitive group from which both felines and machærodonts are derived—the view taken here of their relations.

The basicranial characters of the four genera, *Dirictis*, *Hoplophonus*, *Felis* and *Smilodon*, are contrasted in the accompanying diagram. It is singular, in view of the very marked and profound basicranial distinctions between *Smilodon* and *Felis*, and the importance which has been attached to this region of the skull in the classification of the carnivora, that there should be so few published figures or descriptions and such slight reference to these characters in the later Machærodonts.² The magnificent series of skulls and skeletons of *Smilodon* recently obtained near Los Angeles, California, affords opportunity for an adequate morphologic and adaptive study of this unique and remarkable carnivore. On this account it is not advisable at present to give any detailed discussion of its peculiarities. It represents a highly specialized condition derived from the primitive "Nimravid" type, paralleling the true Felines in a few features, wholly distinct or divergent in others.

VII. *Lower Jaw.* The coronoid process is of moderate height in *Dirictis*, progressively higher and more recurved in *Nimractus*, *Pseudalurus* and *Felis*. In *Hoplophonus* it is much shorter and smaller, and progressively further reduced in *Machærodus* and *Smilodon*. These changes are directly correlated with the reduction and outward twisting of the angle, and with changes in the articulation of the jaw *allowing a progressively wider gape* in the Machærodont phylum, corresponding to the elongation of the canine; while in the Feline phylum the gape is progressively reduced and the articulation of the jaw is strengthened and tightened, to enable the upper and lower canines to bite powerfully in opposition.

¹ See Matthew, 1909, Carnivora and Insectivora of the Bridger Basin. Mem. A. M. N. H., Vol. IX, pt. vi.

² Flower, Mivart and Burmeister refer to them only in a very slight and superficial way; Winge makes a somewhat more definite reference to the peculiar mastoid specialization; but nowhere do I find any reference to the peculiar form and construction of the bulla, quite unlike *Felis* or any of the living Æluroids, and even more unlike the Arctoids. The inclusion of this genus in the Æluroidæ makes it necessary to modify the definition of the group very materially. Yet there seems to be no doubt that its affinities are really with Æluroidæ.

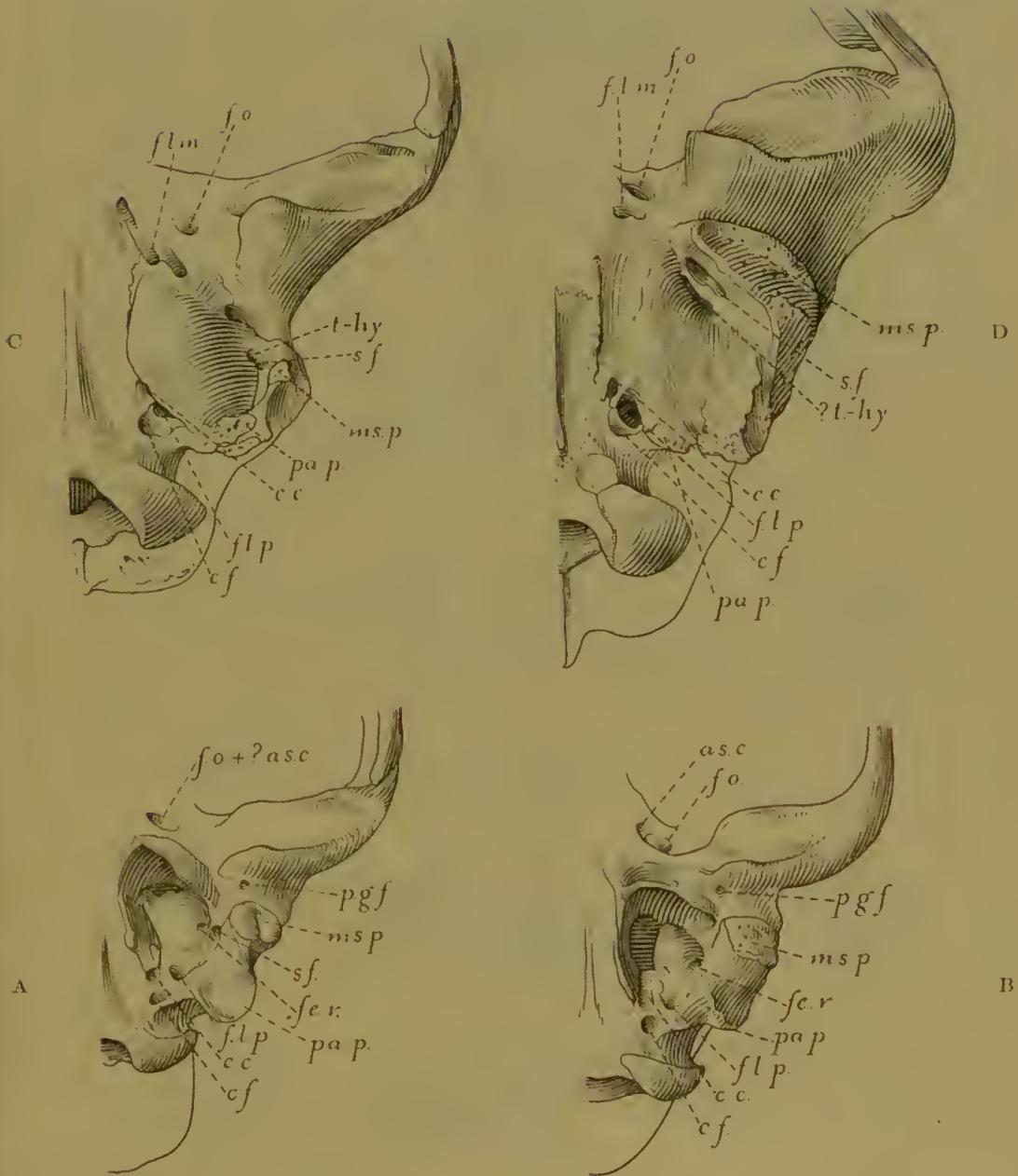


Fig. 6. Basiscranial region in Felines and Machaerodonts. A, *Dinictis*, $\times \frac{3}{4}$; B, *Hoplophoneus*, $\times \frac{3}{4}$; C, *Felis*, $\times \frac{3}{4}$; D, *Smilodon*, $\times \frac{3}{4}$. *As. c.*, alisphenoid canal; *c. c.*, carotid canal; *c. f.*, condylar foramen; *fe. r.*, fenestra rotunda; *f. l. m.*, foramen lacerum medius; *f. l. p.*, foramen lacerum posterius; *f. o.*, foramen ovale; *ms. p.*, mastoid process; *pa. p.*, paroccipital process; *p. g. f.*, postglenoid foramen; *s. f.*, stylomastoid foramen; *t. hy.*, tympanohyal plt.

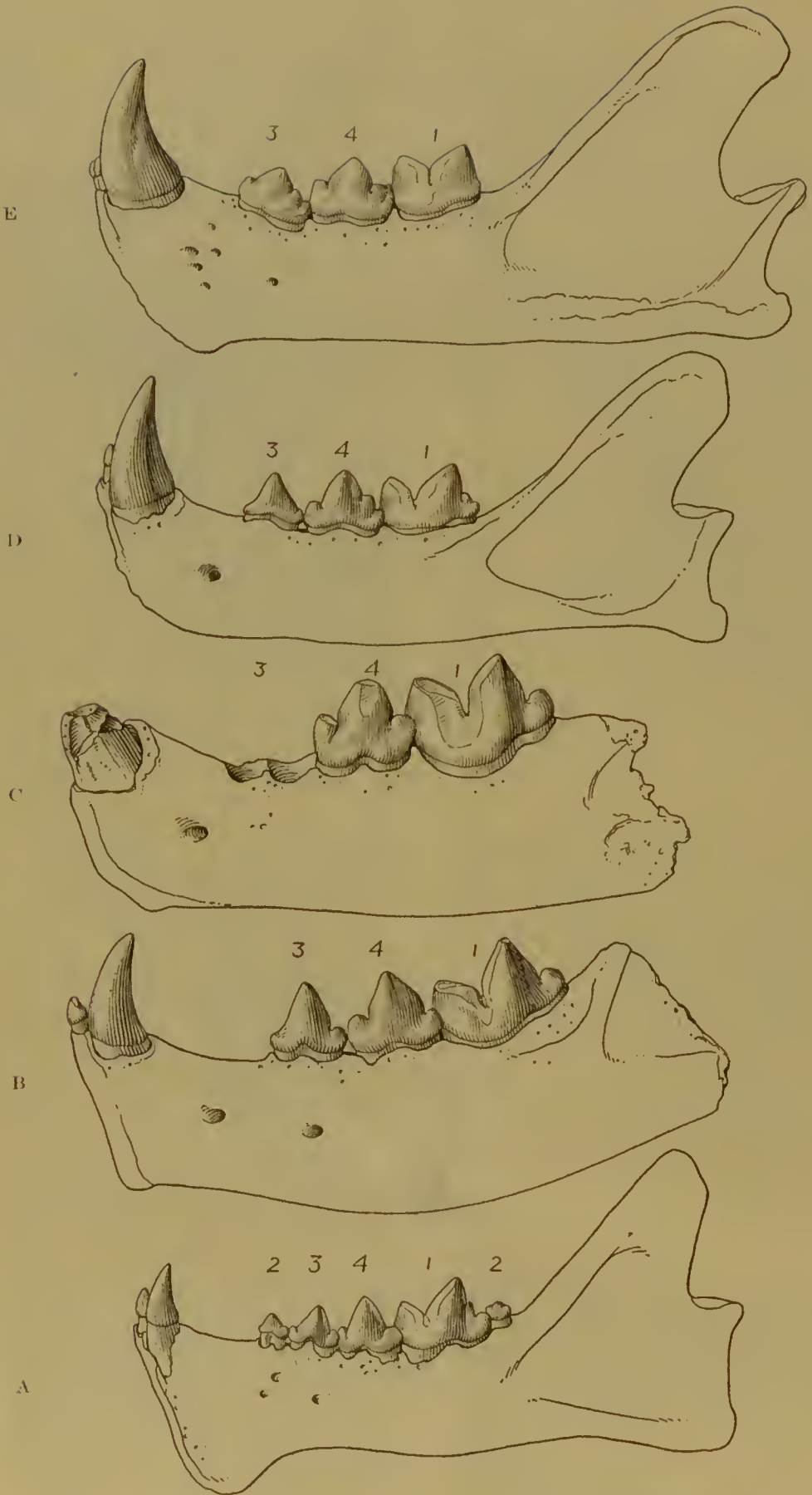


Fig. 7. Feline series, lower jaw. A, *Dinictis*, No. 8777, Middle Oligocene; B, *Nimravus*, No. 6935, Upper Oligocene; C, *Nimravus*, No. 12882, Lower Miocene; [D, *Pseudaelurus*, No. 10396, Upper Miocene; E, *Felis*, No. 11082, Recent. All two-thirds natural size.

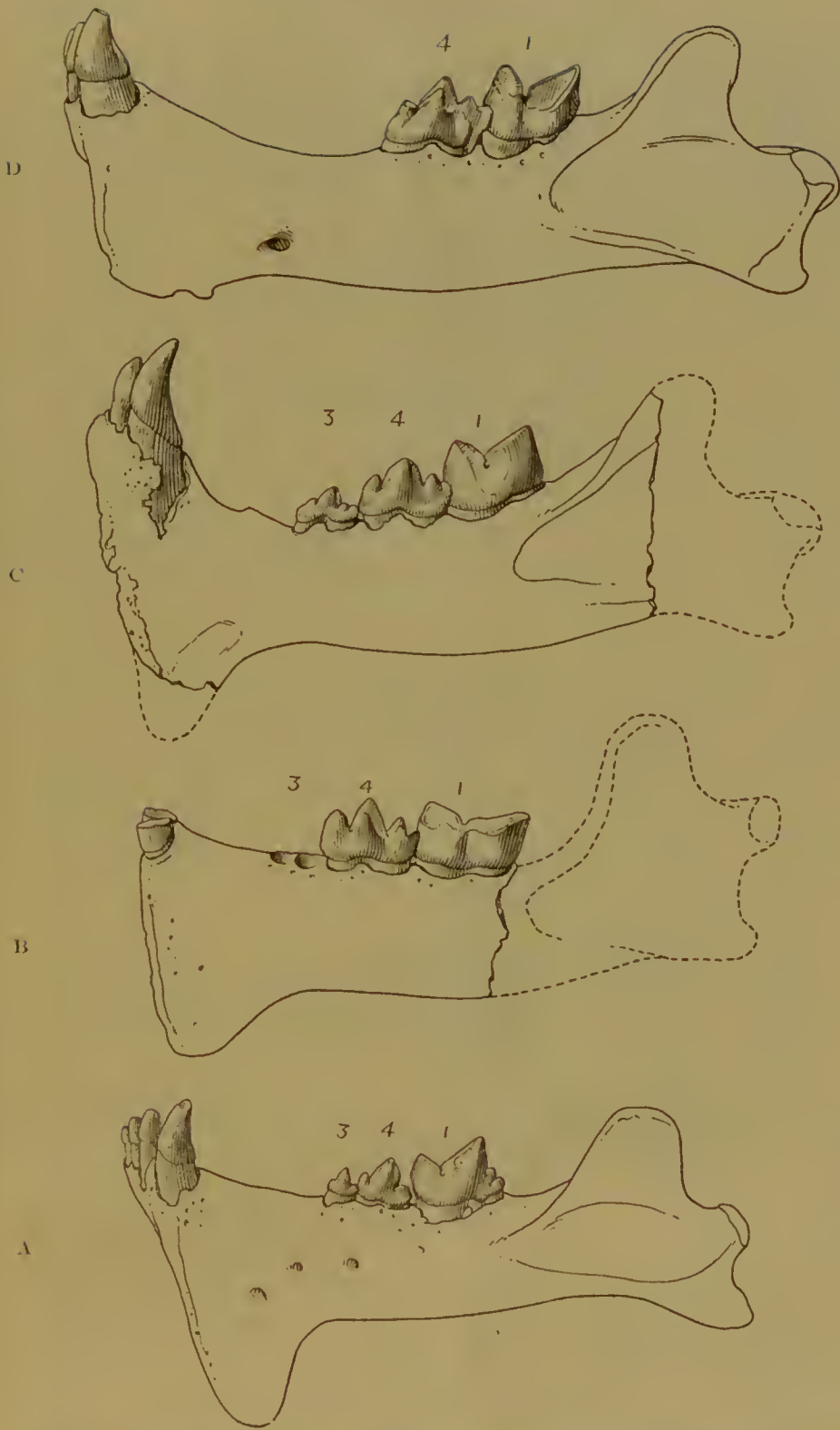


Fig. 8. Macharodont series, lower jaw. A. *Hoplophonus*, No. 11858, $\times \frac{1}{3}$, Oligocene; B. *Macharodus palmidens* (after Filhol and Brule) Miocene; C. *M. megantercon* (after Blainville), Pliocene; D. *Smilodon*, No. 14349, $\times \frac{1}{3}$, Pleistocene.

The lower canines are progressively larger and more powerful in the feline phylum, progressively smaller and weaker in the machaerodont phylum becoming functionally a part of the incisor series.

In considering the significance of these peculiarities in the form and relations of the lower jaw, we may call to mind a few points in regard to the action of the principal jaw muscles.

1. The *temporalis* is the most powerful jaw muscle in Carnivora. It originates from the sagittal and occipital crests and surface of the brain-case, and is attached to the tip and upper part of the coronoid process. Its action is to close the jaws, and it is most effective when the jaw is widely gaping.

2. The *masseter* is the principal jaw muscle in animals with grinding teeth, but is of less importance among the carnivora. It originates on the zygomatic arch (also in front of the arch in rodents and ungulates) and is inserted upon the external side of the jaw below the coronoid process. Its action is to close the jaws and it is most effective when the jaws are nearly closed.

3. The *pterygoid* muscles originate on the inner and outer side of the pterygoids and adjoining parts of skull and are inserted on the inner side of the angle of the jaw in front of and below the condyle. They also serve to close the jaw, acting mainly with the masseter, but with shorter leverage.

4. The *digastric* attaches to the paroccipital process of the skull and to the inferior border of the lower jaw behind the symphysis, and serves to open the jaws.

An inspection of the relations of these muscles shows that in the sabretooth tigers as compared with true cats:

1. Owing to the height between occiput and glenoid articulation, and the short low coronoid process the temporalis was a much longer muscle with much less leverage.

2. The shortness and posterior position of the zygoma, and the weakness of its anterior part, and the more inferior and posterior position of the masseteric fossa, indicate that the masseter was relatively weak and its leverage small.

3. The shortness and outward twisting of the angle increases the length, while decreasing the leverage, of the pterygoid muscles.

4. The relatively high plane of the basicranial region and the downward projections of the glenoid region, with the backward direction of the paroccipital process, serve to considerably increase the length of the digastric muscle, and to enable it to act more effectively when the jaw is very widely gaped.

It will appear therefore that the muscles which close the jaw were of

greater length and less leverage in the sabre-teeth than in normal carnivora, and this is especially true of the temporalis whose chief efficiency is when the jaw is gaping widely. It is a well known and obvious fact in animal mechanics that muscles of great length and small leverage permit

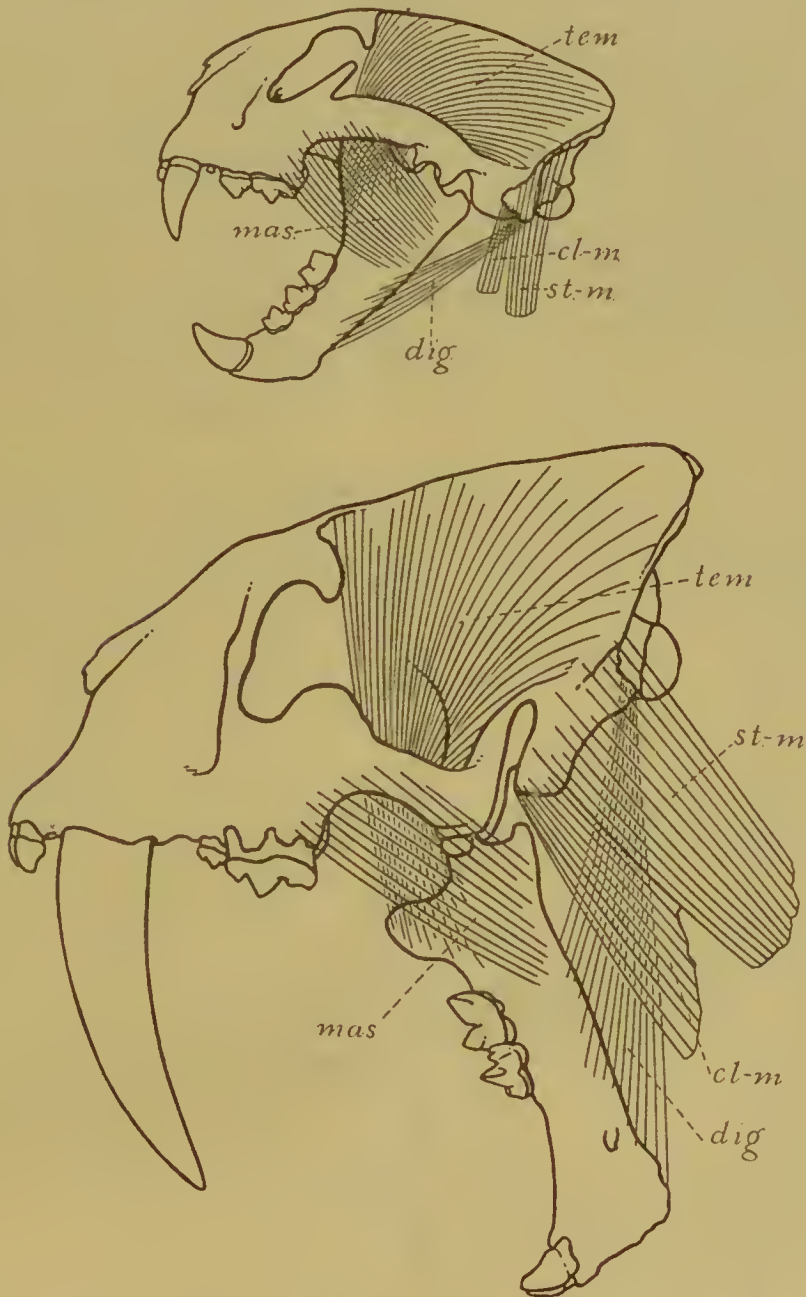


Fig. 9. *Smilodon* and *Felis*. Diagram to show the relations of certain muscles. *Cl.-m.*, clidomastoid; *dig.*, digastric; *mas.*, masseter; *st.-m.*, sternomastoid; *tem.*, temporalis. The skulls are one-fourth natural size, the same specimens shown in Figs. 12 and 15.

an extensive range of motion but lack power; while short muscles of greater leverage are more powerful but limit the range of movement. As a result of the peculiarities cited, the same amount of stretching in the muscles which close the sabre-tooth jaw would permit of a much wider gape than is possible in normal carnivores. We see also that the digastric could draw the jaws much wider open before reaching its limit of contraction.

The gape of the jaws is also limited in normal carnivora by the projection of the angle, which strikes against the posterior surface of the post-glenoid process with any attempt to open the jaws beyond 80° to 90° . But in the Sabre-tooths the outward twisting of the angle prevents its interfering in this way, and the jaws may be swung backward to 150° , when the condyle begins to lift out of the glenoid fossa.

A further adjustment in adaptation to the wider gape of the jaw is seen in the prominence and convexity of the occipital condyles. This enabled the head to be thrown farther back on the neck than in modern Felidae, enabling the jaws to gape wider without interfering with the front of the neck.

Many other adjustments would indeed be necessary in the soft anatomy of the head and neck, to permit of the extreme width of gape necessary for the proper operation of the great tusks of the Machærodont series. But inasmuch as all the adjustments which would leave clear traces in the proportions and construction of the skull are shown to have been present, it seems a safe inference that those which would not leave such traces were likewise present.

VIII. *Proportions of the limbs.* In the Dinictid series the limbs are proportioned much as in the modern felines. In the machærodont series they are much shorter and more robust, approximating the proportions of *Smilodon*.

IX. *Construction of the Feet.* In the primitive members of both series the fore and hind feet are functionally five-toed. In *Dinictis*, however, the inner digit is proportionally more slender than the others, especially in the hind foot. In *Nimrurus* the reduction of the inner digit of the hind foot is carried a little further; in *Pseudalurus* the construction of the feet is not known; in *Felis* the inner digit is vestigial in the hind foot, large but short in the fore foot. The Machærodont phylum, on the other hand, retains the primitive pentadactyl construction even in the hind foot, and in the fore foot the first digit is relatively stouter in all members of the phylum, and progressively so from *Hoplophonus* to *Smilodon*.

X. *Vertebrae, Ribs and Tail.* Both *Dinictis* and *Hoplophonus* retain the primitive proportions of small dorsals, short ribs, long flexible lumbar region, long and heavy tail. In the modern cats these proportions are

preserved to a varying extent; the tail is never so heavy, and may be long or short; the ribs are somewhat longer. The latest of the Machærodonts, *Smilodon*, departs much farther than any of the true cats from this primitive type, in the long and somewhat flattened ribs, the short and relatively small lumbar, indicating loss of flexibility in this region, and in the greatly reduced tail, comparable to that of the bears. *Hoplophoneus* shows no especial approach towards this type in comparison with *Dinictis*, and in *Machærodus* the skeleton is imperfectly known.

There are numerous details in the construction of skull, jaws and skeleton which might be adduced in further support of the relationships here advocated. But the features noted appear to be the most important and to afford adequate evidence that *Dinictis* and *Hoplophoneus* should be regarded as the earliest known stages of two divergent series, one terminating in the true cats, the other in the great sabre-teeth of the Pleistocene.

ADAPTATION OF THE TWO PHYLA.

I suggested some years ago (1901) an explanation of the use of the sabre-tooth canine, regarding the animal as adapted to prey upon the thick-skinned, slow-moving pachyderms — rhinoceroses, suillines, proboscideans, etc., which were the dominant herbivora of the Tertiary period. The elongation of the canines was regarded as adapted to pierce the thick hides of these animals, the method of attack being to strike the head downward with the mouth wide open, and to rip or gash the prey so that it would bleed to death.

The evidence then given in support of this explanation appeared at the time to be sufficient, especially as it could be readily verified and extended by study of material and figures accessible to most students of fossil vertebrates in this country and in Europe. I do not know how generally it has been accepted, but some subsequent writers apparently hold to the old view that the Machærodonts used their canines with the mouth shut, and that they became extinct because they could not open their mouths wide enough to eat. Three eminent authorities (Herluf Winge, Max Weber, O. Abel) have questioned the correctness of the present theory, on the ground that the necessary gape to give play to the canines would cause too great a displacement of the muscles and other parts to be admissible; but none of these writers appears to have considered the proofs which I gave, that the jaws were especially and peculiarly adapted to permit this extreme gape without any undue displacement; nor have they offered any other explanation of the various data adduced in support of my hypothesis. The structural data are more or less fully restated in

the preceding part of this paper. I may add further certain environmental data which accord with it.

As already noted, the dominant and abundant large herbivora of the early and middle Tertiary were of the type which were grouped together by Cuvier as Pachyderms — thick-skinned, short-necked animals, powerful and well adapted for fighting, but not swift footed. During the later Tertiary such animals as the various types of ruminants and the horses became more and more abundant — thin skinned, long legged, slender necked, well adapted for speed, but much less powerful or well armed than the pachyderm type. Meantime the various phyla of pachyderms increased in size, strength, and defensive armor, but dropped off one by one, until now there are only a few survivors, the rhinoceroses, the elephants, tapirs and pigs, and these mostly of limited geographic distribution.

Now the larger eats prey upon the larger ruminants, and smaller cats upon small ruminants et al., and their usual method of attack is to fasten on the back of the animal and bite through the neck until they break or sever the backbone. They are not fitted to, and do not, prey upon such animals as the rhinoceros or the elephant. The great pachyderms have in fact no carnivorous enemies and are kept in check by other means, which are evidently more efficient.

Now if the theory here advocated of the use of the machærodont canine be correct, the sabre-teeths were peculiarly fitted to prey upon large pachyderms, which were well able to protect themselves from other carnivora. Instead of attempting to break or bite through the neck, they would gash or rip it until the animal succumbed. The early felids then, which were all comparatively large and very well armed for attack, were presumably specially adapted to prey upon the early large ungulates, and were all sabre-toothed, as these were mostly of pachyderm type. With the rise and dominance of the large light limbed ruminants and horses some of these early sabre-teeths were correlatively adapted into the modern type of felines; while other sabre-teeths, as the surviving pachyderm phyla became larger, thicker skinned, and more powerful, became progressively larger, more powerful and developed longer and heavier weapons to cope with and destroy them. The final extinction of the Machærodont phylum was probably largely conditioned by the growing scarcity and limited geographic range of the great pachyderms; but other factors must also have been concerned in it.

Another object in reiterating this discussion of the use of the Machærodont canine is to protest against the use of *Smilodon* as an example of the extinction of a race through over-specialization *per se*. That over-specialization can cause a race to be unable to adapt itself to a change of

external conditions or environment, and thus lead to its extinction, will be admitted by everyone. But that a race can continue specializing in some particular direction beyond the point where the specialization is of use, and so far as to cause the actual extinction of the entire race, the environment remaining unchanged, appears to me utterly impossible. The moment the harmfulness of a character outbalanced its usefulness, a process of elimination must needs set in, weeding out the individuals in which the character was mostly highly developed. If such a thing as momentum in evolutionary progress exists, this process of elimination would act with more and more severity, in combating the action of momentum in evolving a character to a noxious degree, with each successive generation. I cannot believe that such a noxious character could be developed to the point of seriously reducing the expectation of life of the individuals in which it was present, much less of being the direct cause of the extinction of the race. Those who have advocated this, to me impossible, theory have repeatedly quoted *Smilodon* as an example in support.¹ In point of fact, as we have seen, the immense development of the canines in this animal made them highly efficient weapons for a particular mode of attack and was an essential element of its success in its especial mode of life, not a hindrance or bar to its survival. Whatever may be thought of the theory of "momentum in evolution," *Smilodon* cannot be used as an instance in its support.

Geological and Geographical Distribution of the Felidae.

		FELINE	MACHÆRODONTINÆ
RECENT		<i>Felis</i> , E., N. A., S. A., As., Af.	
PLEISTOCENE	Upper	<i>Felis</i> , E., N. A., S. A., As. <i>Smilodon</i> , etc., N. A.	
	Lower	<i>Felis</i> , E., N. A., S. A., As. <i>Machærodus</i> , E., <i>Smilodon</i> , N. A., S. A.	
PLIOCENE	Upper	<i>Felis</i> , E., N. A., As.	<i>Machærodus</i> , E., As.
	Lower	<i>Felis</i> , E., As., ? N. A.	<i>Machærodus</i> , E., As.

¹ See Woodward, A. S., 1909, p. 326. Loomis, F. B., 1905, p. 840.

Geological and Geographical Distribution of the Felidæ—Continued.

		FELINÆ	MACHERODONTINÆ
MIOCENE	Upper	<i>Pseudalurus</i> , N. A.	<i>Machærodon</i> , E.
	Middle	<i>Pseudalurus</i> , E., N. A.	<i>Machærodon</i> , E.
	Lower	<i>Nimravus</i> , N. A.	
OLIGOCENE	Upper	<i>Dinictis</i> , <i>Nimravus</i> , N. A.	<i>Hoplophoneus</i> , N. A.
	U. Mid.	<i>Dinictis</i> , N. A.	<i>Hoplophoneus</i> , <i>Eusmilus</i> , N. A.
	L. Mid.	<i>Dinictis</i> , N. A.	<i>Hoplophoneus</i> , N. A.
	Lower	<i>Dinictis</i> , N. A.; <i>Athurictis</i> , E.	<i>Eusmilus</i> , E.
Eocene		(Undiscovered Miacida) probably Asiatic	

CLASSIFICATION AND SYNONYMY OF EXTINCT FELIDÆ.

Earlier writers, and especially Cope, used the presence or absence of the vestigial teeth in defining genera and species in this family, more than their importance or constancy warrants. The form, proportions and construction of the larger functional teeth, especially of the carnassials, appears to be much more constant, and later writers (Scott, Adams, Matthew, Merriam) have admitted the frequent variation in the vestigial teeth as mainly individual. Unless this be done the number of genera and species would be more than doubled.

Felinæ.

Carnassial notches deep; internal cusp of upper carnassial well developed, upper canines progressively reduced and lower canines progressively enlarged to the normal carnivore size and function. Forehead high, mastoid process progressively reduced, coronoid process of jaw enlarged and other progressive changes in skull and skeleton conditioned by reduction of upper canines. P³ large, p₃ and p₄ subequal. Limbs elongate, feet compact, digitigrade, hallux progressively vestigial.

Machærodontinae.

Carnassial notches shallow; internal cusp of upper carnassial vestigial; upper canines progressively enlarged and lower canines progressively reduced, incisiform. P^3 small, P_3 vestigial to absent. Occiput high, narrow,

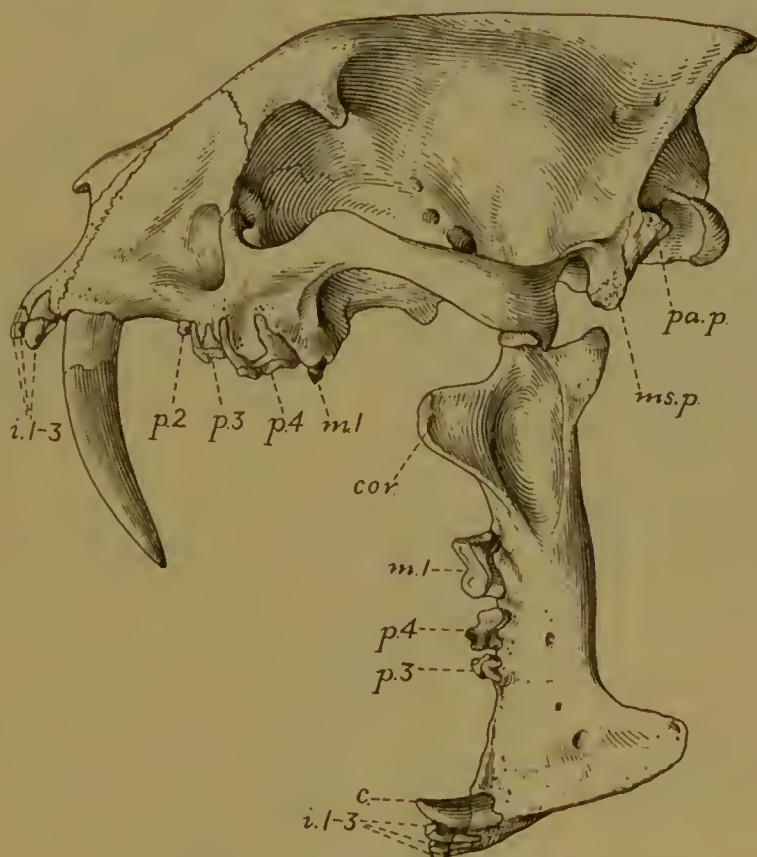


FIG. 10. *Dinictis squalidens*, skull and jaws, one half natural size. Am. Mus. No. 8777. Middle Oligocene, Oreodon Beds, White River, Colorado.

mastoid process prominent, progressively enlarged. Limbs robust, feet more spreading, hallux large, pollex larger than in Felinae.

***Dinictis* Leidy, 1854.**

Dinictis LEIDY, 1854; *Dinictis* auct. plurim.

Syn., *Daptophilus* COPE, 1873.

Dentition normally $I \frac{3}{3}$, $C \frac{1}{1}$, $P \frac{3}{3}$, $M \frac{1}{2}$, but vestigial p^1 and m^2 occasionally present, i_3 ? occasionally absent. M_1 with vestigial metaconid and distinct heel. Canines moderately long, symphyseal flange small. P^4 with distinct protocone and no parastyle. Condylar and carotid foramina well separated from posterior lacerate foramen. Tympanic bulla incompletely ossified. Hallux well developed, functional.

This is a compact genus, the species all nearly related, except *D. cyclops* of the John Day, which is more sharply distinct.

D. felina Leidy, Oreadon Beds, White River, S. Dak. and Col. Typical and most abundant form.

D. squalidens (Cope). Oreadon Beds, White R., S. Dak. and Col. More slenderly proportioned, teeth less robust.

D. paucidens Riggs. White River, Wyoming, horizon unstated.

D. fortis Adams, ? Titanotherium Beds, White River, S. Dak.

D. bombifrons Adams, ? Leptrauchemia Beds, White River, S. Dak.

D. cyclops Cope. John Day Beds, Oregon. Short face, convex forehead.

Nimravus Cope, 1879.

Syn., *Alurogale* Filliol non Fitzinger, *Elurictis* Trouessart; *Archalurus* Cope, *Pogonodon* Cope. Dentition $I \frac{3}{3} C \frac{1}{1} P \frac{1-3}{1-2} M \frac{1}{2}$. M_1 with distinct heel but no metaconid. Canines intermediate between *Dinictis* and *Felis* in proportions, symphysis angulate but flange very slight or none.

Other characters as in *Dinictis*.

This genus covers a much wider range of variation than *Dinictis*, but does not readily fall into subgenera. Several of the species from the John Day beds show a peculiar bony outgrowth beneath the lower carnassial, correlated with a precocious reduction of the upper and enlargement of the lower canines, and designed apparently to shift the support of the lower carnassial outwards in such a way as to afford space for a more powerful masseter attachment than the construction of the skull and jaws would otherwise admit. This constitutes a precocious adaptation functionally analogous to the widening of palate and jaws of the modern Felidae.

N. (Archalurus) debilis Cope. Dentition $\frac{3-1-3-3-1}{3-1-3-2}$. Upper canines but little larger than the lower, symphysis without flange and slight angulation. Bony outgrowth beneath m_1 very prominent. Size medium. John Day.

N. gomphodus Cope. Dentition $\frac{3-1-3-1}{3-1-2-2}$. Upper canines shorter than in *Dinictis*, nearly straight. Symphysis with marked angulation but no flange. Exostosis beneath m_1 slight. Size medium. John Day.

N. confertus Cope. Only the lower jaw is known. Like the preceding species but smaller. John Day.

N. brachyops (Cope). Like *N. gomphodus* and doubtfully separable from it except by absence of the infra-carnassial exostosis. John Day.

N. (Pogonodon) platycopis (Cope). Dentition $\frac{3-1-3-1}{3-1-3-1}$. Upper canines stout, moderately curved. Symphysis with marked angulation and slight flange. No exostosis beneath m_1 . Size large, equalling the lion. John Day.

N. sectator Matthew, 1907. Dentition $\frac{3-1-3-1}{3-1-2-1}$. Symphysis with marked angulation but no flange. No exostosis beneath m_1 . Size intermediate between *N. gomphodus* and *platycopis*. Lower Rosebud, S. Dakota.

N. major (Lucas 1898). From the size and stated characters of *Dinictis major* and its geological level, I suspect that it will prove on examination to be referable to *Nimravus* rather than *Dinictis*. Gering, Nebraska.

N. (Elurictis, Elurogale) intermedia (Filhol). Phosphorites, France.

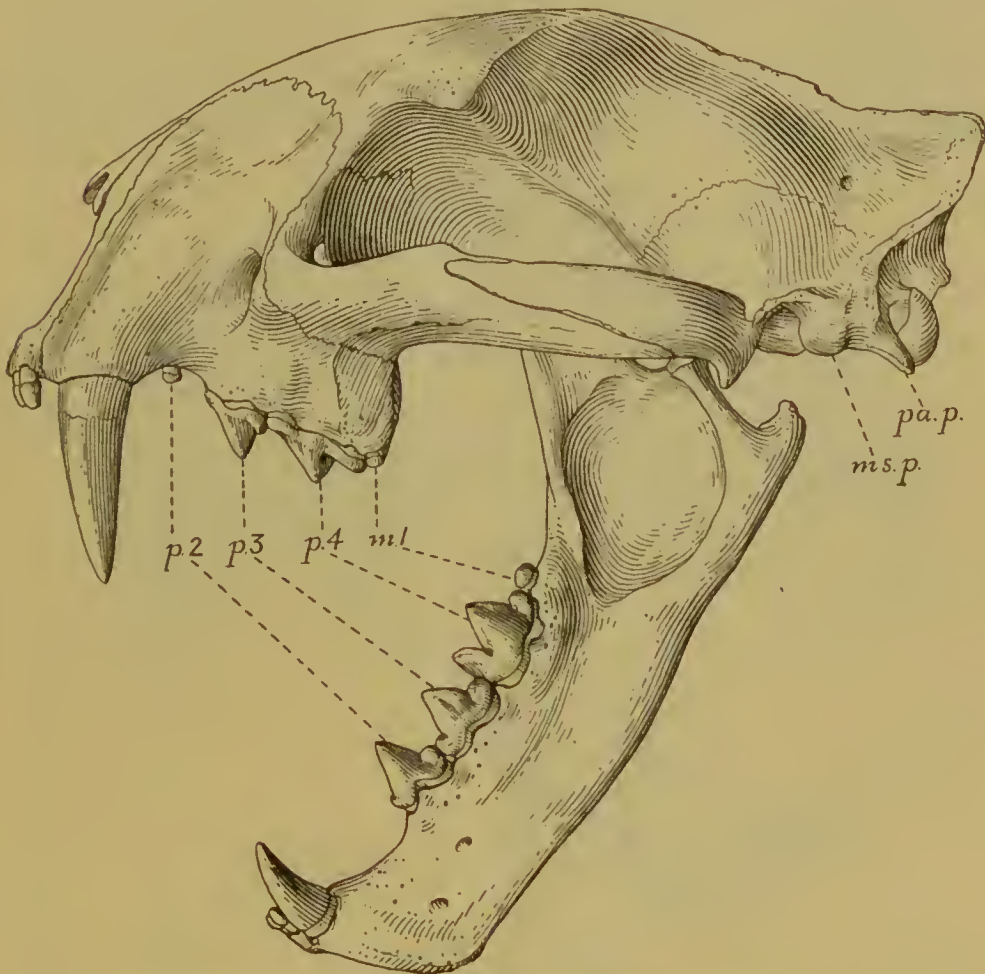


Fig. 11. *Nimravus gomphodus*, skull and jaws, one half natural size. Am. Mus. No. 6933. Upper Oligocene, John Day, Oregon.

N. catocopis (Cope 1887). Size of lion. Known only from symphysis mandibuli, and generic position provisional. Lower Pliocene, Kansas.

Pseudælorus Gervais, 1848-52.

Dentition $I \frac{3}{3}$, $C \frac{1}{1}$, $P \frac{3}{3}$, $M \frac{1}{1}$. Lower sectorial with vestigial heel, no metaconid; upper sectorial with rudimentary parastyle. Canines normal. Symphysis without flange or noticeable angulation. Basicranial and skeletal characters unknown.

P. quadridentatus (Blainville). Middle Miocene (Sansan) France.

P. intrepidus Leidy, 1858. Known only from the lower jaw. Upper Miocene, Nebraska beds, Fort Niobrara, Neb. A lower jaw from the Middle Miocene Pawnee Creek beds of Colorado appears to be a primitive mutation of this species.

Felis s. l.

Dentition $I \frac{3}{3}$ $C \frac{1}{1}$ $P \frac{2-3}{2}$ $M \frac{1}{1}$. Lower sectorial lacking both metaconid and heel, upper sectorial with well developed parastyle. Symphysis without flange or angle.

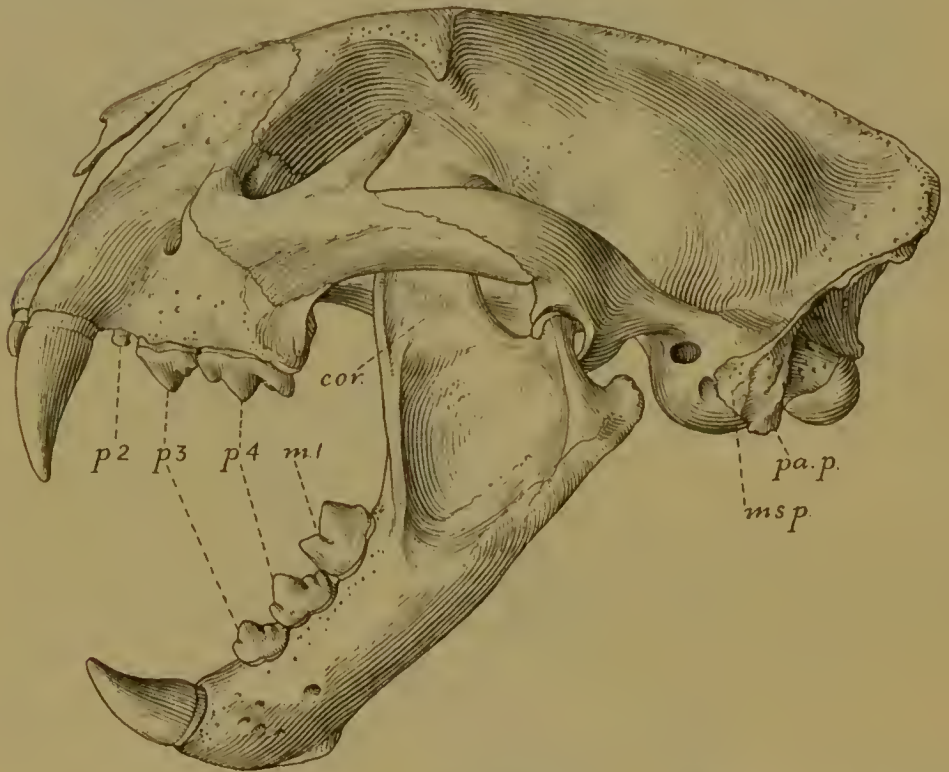


Fig. 12. *Felis concolor*, skull and jaws, one half natural size. Am. Mus. No. 11082. Recent.

Canines normal. Condylar and carotid foramina closely connected with foramen lacerum posterius, tympanic bulla completely ossified. Mastoid process vestigial; paroccipital process directed downwards, flattened and closely embracing the posterior surface of the tympanic bulla. Hallux vestigial.

Hoplophoneus Cope, 1874.

Dentition $I \frac{3}{3}$ $C \frac{1}{1}$ $P \frac{3-2}{2}$ $M \frac{1}{1}$. Upper carnassial with rudimentary parastyle, lower carnassial with metaconid and heel vestigial. P^2 vestigial, p_2 normally absent, $p \frac{3}{3}$ much reduced. Upper canines slender. Basiscranial region as in *Dinictis*, bulla incompletely ossified. Hallux well developed.

This genus is represented by several distinct but rather closely allied species in the White River formation of Colorado and South Dakota.

H. oreodontis Cope. C-M¹ = 53 mm.

H. primævus (Leidy, 1851) C-M¹ = 60 mm. Canines long and slender, skull rather short, p² one-rooted.

H. robustus Adams 1896. C-M¹ = 70 mm. Canines stouter, skull longer, muzzle heavier, p² two-rooted.

H. insolens Adams 1896. C-M¹ = ? 75 mm.

H. occidentalis Leidy 1869. C-M¹ = 92 mm. Skull long and muzzle heavy.

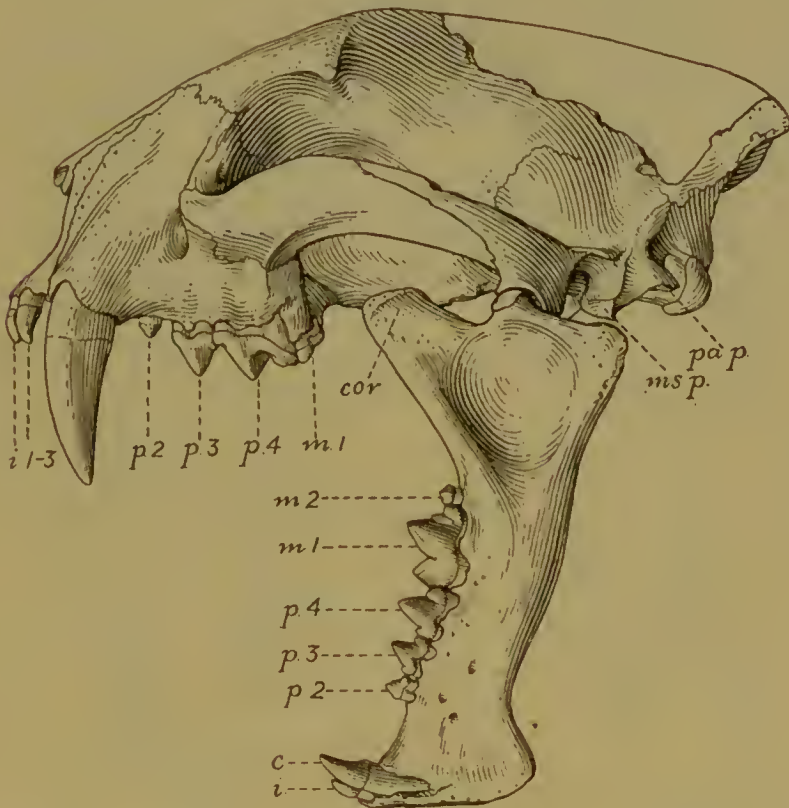


Fig. 13. *Hoplophonus primævus*, skull and jaws, one half natural size. Am. Mus. No. 11858. Middle Oligocene. Oreodon Beds, White River, South Dakota.

"*Pogonodon*" *darvsi* of the John Day appears from Merriam's figures to be referable to this genus and distinct from any of the *Dinictis* phylum.

Eusmilus Gervais, 1876.

Dentition I₂ C₁ P₁ M₁. Lower carnassial without heel or metaconid. Skull unknown. Symphyseal flange deep (= long and slender upper canine).

E. bidentatus (Filliol). Phosphorites, France.

E. dakotensis Hatcher. Upper Oligocene (Protoceras Beds) S. Dakota. Large species, size of lion?

This genus is more progressive than *Hoplophonus*, but apparently out of the direct line of descent.

Machærodus Kaup, 1833.

Dentition $I \frac{3}{3} C \frac{1}{1} P_{2-1}^2 M \frac{1}{1}$. Upper carnassial with well developed parastyle and

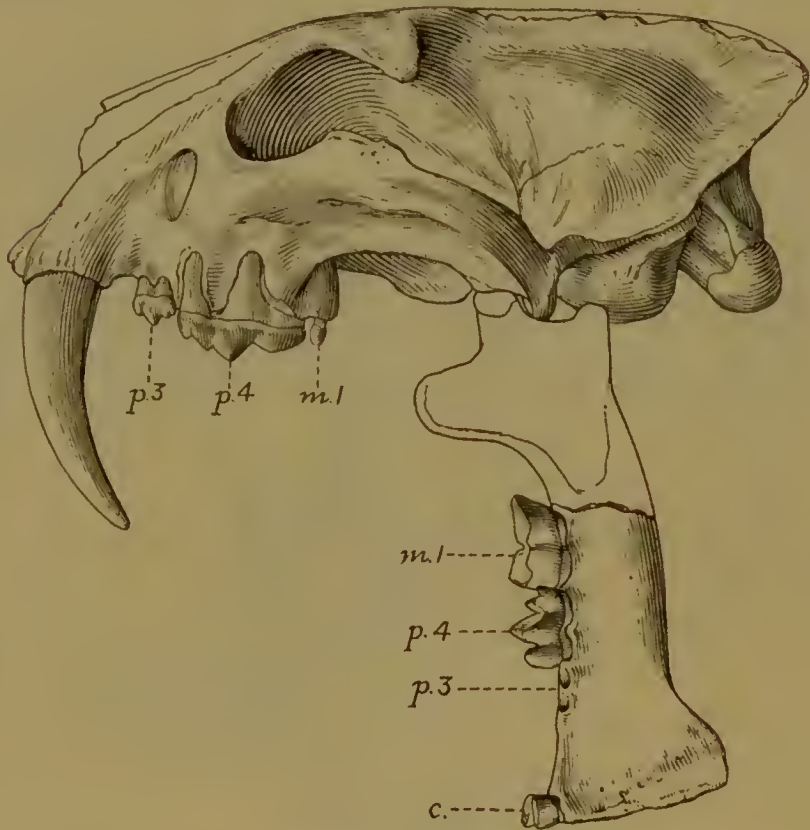


Fig. 14. *Machærodus palmidens*, skull and jaws, half natural size. Middle Miocene. Sansan, France. After Filhol [I suspect certain inaccuracies in this drawing, but do not venture to alter them].

sometimes a fourth external cusp anterior to it. Lower carnassial without heel or metaconid. $P \frac{3}{3}$ vestigial. Canines stout, symphyseal flange deep. Bullæ completely ossified.

European and Asiatic, Miocene to Pleistocene. No recorded specimens from the American Tertiary can positively be referred to this genus.

Smilodon *Lund, 1842.*

Dentition $I \frac{3}{2}$ $C \frac{1}{1}$ $P \frac{2}{2-1}$ $M \frac{1}{1}$. Parastyle of upper carnassial large, fourth cusp variably developed. Lower carnassial without heel or metaconid. Canines large, stout, no symphyseal flange nor angle. P^3 vestigial, p_3 usually absent. Bulla com-

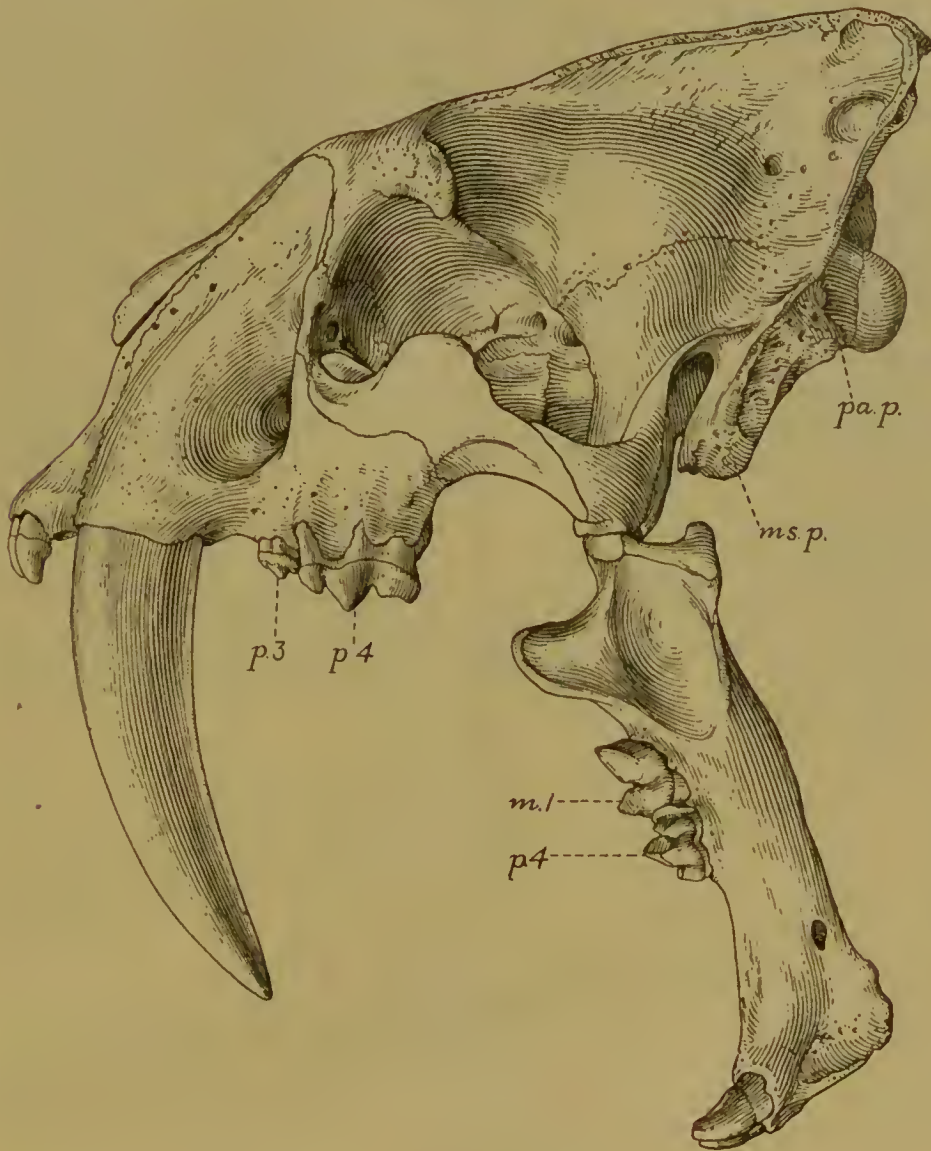


Fig. 15. *Smilodon californicus*, skull and jaws, one third natural size. Am. Mus. No. 14349. Pleistocene, California. (Exchange from Univ. Cal.) *

pletely ossified, condylar foramen distinct, hallux well developed. Several subgenera, all from the New World, so far as records show. The type is from the Pleistocene of South America.

Trucifelis Leidy, 1868. Antero-external (fourth) cusp of P⁴ large.

Dinobastis Cope, 1893. No internal root on p⁴.

Smilodontopsis Brown, 1908. Entepicondylar foramen present.

The later Machærodonts are much in need of revision.

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